Effects of Additional Postcranial Data on the Topologies of Early Eocene Primate Phylogenies

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by

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There are multiple hypotheses regarding the locomotor behaviors of the last common ancestor to primates and which fossil primates best represent that ancestor. These hypotheses rely on morphological and phylogenetic analyses of extinct and extant primate taxa. Two competing conclusions are outlined in Dunn et. al. (2016) and Boyer et. al. (2017). These analyses provide fossil taxa as evidence for their rationale but only the Boyer et al. (2017) research also includes a phylogenetic analysis. Boyer et al.'s (2017) argument relies upon the integration of a new fossil, the talus of *Donrussellia provincialis*, into known datasets, while Dunn et al. (2016) employs the functional analysis of a larger catalogue of fossils from the Vastan mine site. The goal of this research was to conduct a phylogenetic analysis incorporating data from both Dunn et al. (2016) and Boyer et al. (2017). Heuristic tree searches in TNT were conducted on three datasets: one from the Boyer et al. (2017) paper, another that includes just the postcranial elements from Boyer et al. (2017) but with additional taxa and character states, and the final being a combination of the first two. The resulting cladograms show significant differences in topology. All trees present *D. provincialis* as a relatively basal adapiform; more so

in matrices that include craniodental characters. All of the trees whose datasets were expanded to include additional postcranial characters put the Vastan species in primitive positions as well. Adding new postcranial data changed the organization of the cladograms most notably in areas containing Vastan primates and *D. provincialis*. Creating trees from these expanded datasets allows for interpretations and conclusions to be based on results that include all relevant taxa and fossil specimens.

Introduction

Phylogenetic reconstruction is a method harnessed to reconstruct evolutionary relationships among taxa. In some cases, phylogenetic reconstruction utilizes the fossil record as well as an understanding of functional morphology and genetics to achieve this evolutionary understanding. Comparing groups of extinct primates to each other, as well as to extant species, provides a basis for inferring the evolutionary relationships of the primate order. The Eocene epoch represents a time period when early primates proliferated due to increases in temperature (Gingerich 2012). There have been numerous phylogenetic analyses assessing the phylogenetic position of Eocene primates (e.g., Boyer et al. 2017; Chester et al. 2015; Morse et al. 2019; Ni et al. 2013; Rose et al. 2009). Many primate and mammalian phylogenetic studies in general focus heavily on craniodental morphology (Spaulding and Flynn 2012). This strategy is somewhat out of necessity, as the information known about early primates comes from the fossil record, which disproportionately contains easily preserved elements, which in the case of mammals is usually teeth (Mounce et al. 2016). Within cladistic studies of many mammalian lineages there seems to be a pattern of favoring craniodental elements, though analyses of different phylogeny subsets have shown that neither post-cranial or craniodental data is more or less homoplastic than the other (Mounce et al. 2016; Sánchez-Villagra and Williams 1998). In fact, the addition of postcranial elements to datasets can lead to more resolved resulting trees (Spaulding and Flynn 2012). Also, the postcranial morphology can provide answers to questions related to locomotion, a key aspect in many evolutionary hypotheses.

Some have proposed that trees containing only molecular data are more informative and can be used to identify homoplasy within morphologically based trees (Gaubert et al. 2005). Using molecular information is difficult for early primate analyses as these trees rely on the morphological data for the character states of extinct taxa. The reliance on incomplete catalogues is a major issue not just in terms of missing fossil data but also in terms of missing data other than fossils. Recent research has shown that a relative lack of soft-tissue evidence can also distort the results of a cladistic study, specifically in terms of the hypothesized timing of different evolutionary transitions (Sansom and Wills 2013). Using all data available when developing a cladogram is the method that is considered to provide the most reliable results, but looking at subsets of morphological elements can provide a method of comparison (Mounce et al 2016). Due to the fact that the fossil record is incomplete, phylogenetic analysis is subject to change, and often, with newly discovered fossils come different phylogenetic interpretations.

The discovery of early fossil primates has led to multiple hypotheses describing possible characteristics for the last common ancestor of the primate order. Different theories often focus on primate morphological traits and try to provide an adaptive explanation for their appearance within the mammalian lineage (Fleagle 2013). Some early theories are focused on the movement to arboreal habitats being the main factor in the evolution of crown primate adaptations (Clark 1960). Connecting traits to behaviors or ecology can present many examples of convergent evolution, and many have pointed out that there are other arboreal mammalian lineages that lack the catalogue of crown primate features (Cartmill 1974). So, theories regarding the emergence of primates have

become more specific in defining the ecological factors that surrounded said emergence. For example, the “Visual Predation Hypothesis” posits that the primate ancestor utilized both enhanced visual features and arboreal grasping adaptations to catch insects as prey (Cartmill 1974). This theory explains the adaptive benefit of both cranial and postcranial features. Another diet-focused hypothesis attributes the crown primate features to coevolution with angiosperms (Sussman 1991). Both hypotheses consider ecological factors to some extent.

Some hypotheses connect primate origins with specific locomotor specializations brought about by certain environmental factors. One key hypothesis suggests that the last common ancestor to crown primates possessed a "grasp leaping" pattern of locomotion, which is something that is still seen frequently within extant primates (Szalay and Dagosto 1980). This type of behavior would have been used to move quickly in an arboreal environment, which is different from the slow and careful locomotion which aligns more with the alternative "Small Branch Niche" hypothesis (Cartmill 1974; Lemelin and Schmitt 2007). There is a great deal of debate surrounding which theory is the best supported, as well as how contributing data should be interpreted. There is not a representative species for the last common ancestor of crown primates from the Paleocene, which is the epoch during which the common euprimate ancestor is hypothesized to have evolved (O’Leary et al. 2013). The lack of a morphological model for this ancestor is something that significantly hinders the current understanding of primate origins. Therefore, it becomes critical to know the phylogenetic relationships

among early primates, as a means of getting closer to answering questions about primate origins.

Boyer et al. (2017) provided evidence to support the theory that leaping adaptations evolved within primates before adaptations for climbing on small branches. The new data emerged in the form of the *Donrussellia provincialis* talus. This species was previously only known through craniodental fossil elements. This species is regarded as being one of the most basal taxa that has been discovered within the primate order because of its primitive dental characteristics (Godinot 1998). Boyer et al. (2017) analyzed this new talus of *Donrussellia* in two ways, morphologically and phylogenetically. First, using Principal Components Analysis (PCA), the new talus was functionally analyzed and compared against a large group of other tali to determine to which group the *D. provincialis* talus is most similar, as well as to identify its most statistically relevant features. Specific features pertaining to the fibular facet, the medial tibial facet, and flexor fibularis groove were measured for one PCA analysis. The other PCA analysis used data encompassing the entire talar body of 161 specimens. For both analyses, the species included plesiadapiforms, omomyiforms, adapiforms, and extant primates. Boyer et al. (2017) concluded that the *D. provincialis* talus is primitive, as evidenced by its morphological similarity to the primate sister groups treeshrews (specifically *Ptilocercus lowii)* and plesiadapiforms. However, there were also certain features that aligned *Donrussellia*'s talus with omomyiforms and adaptations associated with leaping behaviors. The tree shrew and plesiadapiform-like features such as a flexor fibularis groove that is positioned laterally, a "steep talofibular facet and a relatively

small medial tibial facet", and a talar head that is relatively more transverse were proposed to favor large diameter rather than narrow supports (Boyer et al. 2017). Some important features that aligned the specimen with omomyiforms, pointing to a leaping form of locomotion, were the appearance of a squatting facet, and an elongated talar neck (Boyer et al. 2017). Boyer et al. (2017) used this array of features on the talus as evidence to support the hypothesis that leaping behaviors evolved in primates before the use of small branches. These interpretations were combined with the results of the phylogenetic analysis to inform the final conclusions of the research.

The cladistic study within Boyer et al.'s (2017) research was conducted by adding the new postcranial information from the *D. provincialis* talus into two existing phylogenetic matrices. One such matrix came from Ni et al. (2016) and included a very large set of morphological, as well as molecular information. Once the *D. provincialis* talus was added, the species moved into a position that was more basal compared to other adapiforms. The other matrix was from Boyer et al. (2016). It included craniodental and postcranial data but lacked molecular information. The addition of character states from the *D. provincialis* talus (as well as for *Purgatorius unio*) changed this cladogram as well. In the initial version when only craniodental data were included for the *D. provincialis*, the species appeared as more basal than all primates and plesiadapiforms. When the new character states for the talus were included, *D. provincialis* moved to a position nested within the crown primate group and in a clade with *Cantius* that is basal to other adapiforms. Boyer et al. (2017) concluded that *D. provincialis* is an extremely primitive primate and most likely the most primitive adapiform. Moreover, they concluded that the

locomotor interpretations drawn from *D. provincialis'* talus are likely to be representative of the locomotor behaviors of the last common ancestor to primates. Therefore, Boyer et al.' s (2017) cladistic and morphological analyses suggested that adaptations to leaping in primates preceded locomotor adaptations to the small branch niche.

Dunn et al. (2016) also posited that certain species are representative of the last common ancestor to primates, at least in terms of locomotor adaptations. The focus of the article is the morphological analysis of new fossil specimens discovered in the Vastan mine site in Gujarat, India. While Dunn et al. (2016) introduced specimens that were not included in the Boyer et al. (2017) analysis, Dunn et al. (2016) did not provide a phylogenetic analysis. Rather, the basis for the Dunn et al. (2016) locomotion hypothesis was previously determined phylogenetic relationships as well as morphological comparisons with other species. The large group of specimens discussed in this paper are all postcranial, and if they were designated to a species, it was an already known primate species from the Vastan area. This group of taxa includes two asiadapids: *Asiadapis cambayensis*, and *Marcgodinotius indicus*, and two omomyids of the same genus: *Vastanomys major*, and *Vastanomys gracilis*. Interestingly, when grouped by size, *A. cambayensis* and *V. major* are more similar, in that they are larger than the other two. There was already some postcranial material known for the asiadapid group described in Rose et al. (2009) that was useful for allocation of the new fossils, as well as for the descriptions of the previously unknown specimens.

Dunn et al. (2016) agreed with the earlier phylogenetic conclusions of Rose et al. (2009) that Asiadapidae (the subfamily composed of *Asiadapis* and *Marcgodinotius* taxa)

is one of the most basal groups of adapiforms. Dunn et al. (2016) focused on functionally interpreting the new fossils within the context of what is already known about the taxa they represent and using these conclusions to describe the probable features of the primate last common ancestor. The asiadapids exhibit femora with patellar grooves that are defined and narrow, thin peroneal tubercles in the metatarsal, and a lack of calcaneal elongation (specifically for *M. indicus*) all pointing to generalized arboreal forms of locomotion (Dunn et al. 2016). As for the *Vastanomys* group, the postcranial elements are described as more generalized than most omomyiforms and similar to Asiadapidae. The *Vastanomys* specimens display some leaping features such as proximally located lesser and third femoral trochanters relative to the asiadapids, and medially and posteriorly flattened borders and a posterolaterally expanded articular surface of the femoral head (Dunn et al. 2016). However, these traits do not reach the levels that are seen in other omomyids, for example, the distal intercondylar fossa is relatively shallow compared to other tarsiiforms (Dunn et al. 2016). The humerofemoral index is also larger than in living and extinct leapers and point toward quadrupedal behaviors (Dunn et al. 2016). The main functional conclusions of Dunn et al. (2016) are that *Vastanomys* and the asiadapids have relatively similar and generalized postcranial features. Therefore, Dunn et al. (2016) concluded that the physical similarities between the two groups could be plesiomorphic traits that would have also been seen in the primate common ancestor or could be due to a reversal of more specialized traits. Dunn et al. (2016) hypothesized that the similiarities are most likely primitive retentions, representing a more parsimonious path. Also, taking into account that the Vastan taxa were contemporaneous, it makes

more sense that these generalized locomotor traits did not evolve separately in the two groups to differentiate function and niche but are rather shared primitive traits.

The goal of this project was to merge the phylogenetic techniques and talar data of the Boyer et. al. (2017) research with the postcranial fossil specimens from Dunn et al. (2016), and other prominent early primate specimens, to reevaluate which species should be considered more primitive within primate phylogeny. The phylogenetic dataset from Boyer et al. (2017) does include the asiadapid specimens from Rose et al. (2009), but not any of the new fossils introduced in Dunn et al. (2016). *Vastanomys* does appear in the functional analysis (the PCA of talar data) but was not included in the phylogenetic analyses of Boyer et al. (2017), so its phylogenetic placement remains unclear. Similarly, *Notharctus tenebrosus* and *Smilodectes gracilis*, two prominent adapoid species were not already within the Boyer et al. 2017 matrix though they have been described previously (Gregory 1920). Another group of fossil primates was added to the taxon list for this phylogenetic analysis as well. These include *Ourayia uintensis*, *Chipetaia lamporea* and *Mytonius hopsoni,* which appear within Boyer et al.'s PCA analysis but were not included in their phylogenetic analysis. This group was functionally interpreted by Dunn et al. (2006; 2010). These species serve a different purpose in that rather than representing taxa close to the base of the tree, these three appear in the late middle Eocene, and most likely relied on leaping adaptations (Dunn 2010). It is also interesting because these species represent a group of euprimates that are larger in body size. The addition of these three taxa not only increases the number of specimens within the cladistic matrix, thus increasing its probability of representing the true phylogeny, but it

also provides a very interesting comparative context for *D. provincialis*. With this expanded taxon list, multiple phylogenetic analyses were done, each looking at different subsets of the characters in the original matrix provided by Boyer et al. (2017).

Methods

Out of the two cladistic matrices used in the Boyer et al. (2017) analysis, the smaller one (initially from Boyer et al., 2016), includes only morphological data. Therefore, this was the matrix that was chosen as a starting point for my analysis. As discussed above, a dataset from Boyer et al. (2016) was edited by Boyer et al. in 2017 to contain newly attained talar information for *D. provincialis* and character scores for the talus and calcaneus of *P. unio* to make a slightly modified dataset. This dataset from Boyer et al. (2017) will be referred to as Matrix A. It is included here primarily as comparison for the other datasets and trees, but also because the resulting strict consensus tree was slightly different than those seen in Boyer et al. (2017). For the second dataset, which is a postcranial-only matrix (Matrix B), the character list from the Boyer et al. (2017) dataset was reduced to only those that described the elements that were allocated to species from the Vastan mine site and analyzed by Dunn et al. (2016). Those elements are the humerus, the talus, the calcaneus, the tibia, the femur, and metatarsal I. For each of these, there was at least one newly analyzed fossil specimen described in Dunn et al. (2016), but not originally scored in the Matrix A. The taxa list was also reduced to include only the Boyer et al. (2017) matrix (Table 2). Therefore, any species that only had craniodental characters scored, or only characters pertaining to another postcranial element were removed from the matrix. There were twenty-five characters associated

with postcranial elements other than the ones Dunn et al. (2016) analyzed for the Vastan species. These were excluded from the postcranial-only dataset because the focus of that analysis was to look at how the additional specimens from Dunn et al. (2016) affected the phylogenetic organization with and without other elements. The third and final dataset (Matrix C) represents the addition of the postcranial dataset (Matrix B) to Matrix A.

Seven new taxa were then added to both Matrix B and C: *V. major*, *V. gracilis*, *N. tenebrosus*, *S. gracilis*, *O. uintensis*, *C. lamporea*, and *M. hopsoni*. The two Vastan asiadapids (*A. cambayensis* and *M. indicus*) were already in the taxon list but lacked character states for some of their newly discovered elements outlined in Dunn et al. (2016). Therefore, those two taxa were edited to include additional character states. Due to the increase in the number of talus and calcaneus specimens for these two species compared to what was in Matrix A initially, some of the characters pertaining to average measurements were adjusted. The qualitative characters for these elements stayed the same, however. The other elements for the asiadapids were newly discovered and their character states were scored and added in as were those of the other additional taxa. The scores for the added or edited character states of these nine taxa were obtained from either the primary literature describing them, their digital images available on Morphosource.org, or from measurements also provided by primary literature (See Table 2 for citations relevant to specific taxa). The exact sources for any character states that were edited are also outlined in the annotations of the Nexus file for this cladogram which is available in the Supplemental data along with the links to the Morphosource

used. Table 1 summarizes the full taxon list for this research and shows which species are contained in each dataset.

The trees for this research were created following methods outlined in Ni et al. (2016) using version 1.5 of TNT ("Tree Analysis using New Technology") software (Goloboff and Catalano 2016). The TNT command line used to calculate the set of most parsimonious trees is available in the supplemental data for my project. Even though Boyer et al. (2017) used PAUP for the analysis of Matrix A in their research, TNT was used for this project as it is a quicker, more easily accessible program. Matrix A was rerun first in order to ensure that the process would provide comparable results to the original phylogenetic analysis performed in Boyer et al. (2017). Subsequently, the other two datasets (Matrices B and C) were run in TNT. All of the datasets were constrained by a molecular scaffold provided by Boyer et al. (2017), which represented the known molecular relationships among all of the extant species included in the dataset. The TNT command lines used for this scaffold are included in the supplementary data. Majority trees and strict consensus trees were obtained for each dataset, and 1000 replicate bootstrap analyses were then run on each in order to investigate the quality and confidence surrounding them (see Table 3).

Results

The resulting trees (Figures 1-4) from each dataset show certain similarities. All trees in this analysis have *Tupaia glis* as the outgroup as in the original Boyer et al. (2017) matrix tree, and in all trees, the plesiadapiforms form a monophyletic clade as the sister group to the euprimate clade. With the molecular scaffold, the extant species are

positioned as expected in the cladogram. In all but the Matrix B tree, omomyiforms form a clade with tarsiids (extant and fossil) that is a sister group to anthropoids and thus in this analysis, omomyiforms will be referred to as stem tarsiiforms. For Matrix B, there are some stem anthropoids within the omomyiform and tarsier monophyletic group, and *Steinius* appears in a clade with extant platyrrhines (discussed in more detail below). For Matrix A and Matrix B, the strict and majority consensuses are very similar, so interpretations are from the strict trees and are shown in the Figures 1a, 1b, 2a, and 2b. Matrix C however showed some interesting differences between the majority and strict consensus outputs, especially where the added taxa are concerned, so both are included in the text as Figures 3a, 3b, 4a, and 4b. All three matrices resulted in trees with key differences among them that are outlined below.

The tree from Matrix A (Figures 1a, 1b) aligns fairly well with the tree reported from the original use of the data (Boyer et al. 2017). The large monophyletic groups in the original tree and the Matrix A tree have the same taxa within them but differ slightly in topology. One exception is that in Matrix A, *Rooneyia viejaensis* is nested within anthropoids rather than with other omomyiforms as found by Boyer et al. (2017). *Rooneyia viejaensis* can be seen nested within a monophyletic group with fossil anthropoids in Figure 1b. Aside from *R. viejaensis,* the anthropoid group includes the same taxa as in the Boyer et al. (2017) and still places *Eosimias centennicus* in the most basal position. There are other minor differences due to the fact that it is a less resolved strict consensus tree than what is seen in the Boyer et al. 2017 Figure S4. These variations are most likely due to the slightly different tree search done and the different

programs used. The area of the cladogram that is most important for the implications laid out in Boyer et al. 2017 is the same for the original and the rerun trees of Matrix A. As in Boyer et al. (2017), *D. provincialis* forms a clade with *Cantius abditus* and *Cantius ralstoni,* and that clade is the sister group to a large clade containing all other adapiforms as well crown strepsirrhines. The asiadapids are also still nested within that large clade of adapiforms but form a polytomy with a clade containing *Hoanghonius stehlini* and *Renicunius zhoui* rather than being placed in slightly more derived position as seen in the Boyer et al. (2017) tree.

Matrix B included only postcranial characters. Similar to the Matrix A tree, two large monophyletic groups emerge in the primate clade. The tarsiiform clade is made up mostly of omomyiforms and tarsiids (extant and fossil) while the other is mostly adapiforms and strepsirrhines. When the data are restricted to these certain postcranial elements, *D. provincialis* still forms a clade with both *Cantius* species (as in Matrix A), however *D. provincialis* is now sister to *C. ralstoni,* making the two *Cantius* species paraphyletic. In addition, as in Matrix A, the clade containing *D. provincialis* and *Cantius* is sister to the clade formed by the remaining adapiforms and crown strepsirrhines. However, unlike Matrix A, in Matrix B the asiadapids form a clade positioned basal to the rest of the adapoids and all extant strepsirrhines. In Matrix B, *V. major* is placed as the most basal omomyid, but oddly is not grouped with the other species of its genus. *V. gracilis* (which only contains character states for a humerus) is a sister taxon to the adapiform and strepsirrhine clade (which includes the Vastan asiadapids). As for the other taxa added to Matrix B, *N. tenebrosus* and *S. gracilis* form their own clade that is in

a polytomy with the other adapoids (excluding the asiadapids, *D. provincialis,* and *Cantius* species) and all extant strepsirrhines. The three additional species from the Uintan basin are placed in the tarsiiform clade that contains all of the omomyiforms (with the exception of *Steinius* discussed below) as well as the *Dolichocebus gaimanensis, Eosimias centennicus* and *Tarsius bancanus,* an extant tarsier (Figure 2b). *O. uintensis* and *C. lamporea* form a polytomy in a derived position of that clade with the extant tarsier, while *M. hopsoni* falls just outside of that clade in another polytomy. All three Uintan taxa are in a clade to which *Shoshonius cooperi*, an omomyoid, is the sister taxon.

There are three taxa that fall relatively far from their expected phylogenetic placement. These are the *Steinius spp., D. gaimanensis and E. centennicus* (see Figures 2a and 2b). *Steinius,* an omomyiform, is placed within the extant platyrrhines, specifically it is shown to be a sister taxon to *Alouatta seniculus*. *D. gaimanensis* and *E. centennicus* are both shown to be unresolved within the tarsiiform clade (see Figure 2b). *D. gaimanensis* has been placed as a stem platyrrhine as well as a crown ceboid, so it is interesting that it is placed with omomyiforms (Kay et al. 2008; Rosenberger 1979). Similarly, *E. centennicus* has been categorized as a fossil anthropoid not an omomyiform (Beard et al. 1996). The unexpected placement of these three taxa may be due to the fact that each were represented by only one postcranial element in Matrix B: the talus. Therefore, without any craniodental data included in the matrix, these taxa, like *D. provincialis,* only have scores for the talus characters.

The trees derived from Matrix C are the most inclusive cladograms for this research as they contain the most characters and taxa. The strict consensus tree (Figures

3a and 3b) places *D. provincialis* at an extremely primitive position, but it is placed in a polytomy with *Vastanomys,* the asiadapid clade, and the monophyletic group containing all other adapiforms and extant strepsirrhines. It is interesting to note that both of the omomyiform Vastan primates are grouped with adapoids in this tree. *R. viejaensis* is once again in an odd position, but it now appears as a sister taxon to adapiforms rather than nested within anthropoids. In the clade nested deep to *R. viejaensis,* all adapiforms (except *D. provincialis* and the Vastan asiadapids) fall in a polytomy with a monophyletic group that contains fossil and extant strepsirrhines. The monophyletic strepsirrhine clade has the exact same topology as the one within the Matrix A tree. The fossil strepsirrhines here include stem galagids such as *Komba* species*, Saharagalago misrensis,* and *Wadilemur elegans* and stem lorisids *Nycticeboides simpsoni* and *Karanisia clarki,* with the rest of the clade being made up of extant strepsirrhines (Jacobs 1981; Seiffert et al. 2005). *K. clarki* is in the most basal position of the clade, and the other stem lorisid, *Nycticeboides simpsoni*, falls within a clade with the extant lorisids. The three stem galagids are all placed basally within the galagid clade. This clade is one of the best examples in this analysis of a monophyletic group that aligns well with current cladistic theory. *N. tenebrosus* and *S. gracilis* are both nested within the adapiform polytomy along with a *Cantius* clade (Figure 3b). All three Uintan species are nested within the clade containing stem and crown tarsiids, and, somewhat similarly to the Matrix B tree, *M. hopsoni* is unresolved while *O. uintensis* and *M. hopsoni* form a monophyletic group that is also rather unresolved in its clade position. The anthropoid clade contains stem anthropoids as well as extant and stem catarrhines and platyrrhines.

The majority consensus tree for Matrix C (with a cutoff of 50), is slightly more resolved than the strict consensus tree, and is pictured here because of the differences in how it positions *Donrussellia* in relation to the taxa added from Dunn et al. (2016). In the majority consensus tree, asiadapids form a sister clade to a *Vastonomys* clade, and *D. provincialis* is placed basal to that asiadapid-*Vastonomys* clade (Figures 4a and 4b).

Discussion

The addition and partitioning of data to the matrices led to differences in the topologies of the resulting trees. Matrix B was different from the original dataset's tree most obviously in the placement of *D. provincialis*. By only analyzing the postcranial characters, the clades shifted quite a lot. Instead of *D. provincialis* appearing as the most basal adapiform, the asiadapids are in this position. Also, the fact that the most problematic taxa are those that only include talar data within Matrix B, makes interpreting *D. provincialis* in this tree less reliable. One odd feature of the Matrix B tree is the placement of *V. gracilis* with adapiforms rather than omomyiforms and *V. major*, which is most likely due the fact that the postcranial data of *V. gracilis* is limited to the humerus. This particular element is described as difficult to allocate and functionally analyze for early primates due to the lack of a large comparable sample (Dunn et al. 2016). *V. major* is positioned as very primitive within the stem and extant tarsiid clade. This placement is interesting when compared to the *V. major* position in Matrix C's trees where both *Vastanomys* taxa fall with basal adapiforms. The trees resulting from Matrix B diverged from those of Matrix A much more than did those resulting from Matrix C

and those from Matrix B had more oddly placed taxa. Therefore, Matrix B doesn't hold the same weight in terms of providing evidence compared the results of Matrix C.

Overall, the set of trees from Matrix C may be the best representation of phylogeny as it contains the most characters being analyzed (Mounce et al. 2016). Not only are the new osteological elements from the Vastan mine sites integrated into a large preexisting dataset, but the addition of other omomyiform and adapiform postcrania that fall into their expected places helps strengthen the expanded matrix. In the Matrix C trees, *D. provincialis* is in a position more similar to the Matrix A cladogram. However, the asiadapids move closer to the root of adapiforms with the addition of their postcranial data from Dunn et al. (2016). Near the base of the adapiform and strepsirrhine clade is also where the two *Vastanomys* species that were added are placed. The position of the Vastan primates in the Matrix C trees suggest that they could be representative of the stem strepsirrhine condition. However, if craniodental characters were added for *Vastanomys*, the topology would likely change, just as there was a difference when craniodental characters were taken out of the dataset. All trees containing the new data (Matrix B and Matrix C) show that *D. provincialis* and the four primate species from the Vastan mines are very primitive, though only postcranially in terms of *Vastanomys*. The cladograms resulting from the analysis of Matrix C, especially the majority tree, support the Boyer et al. (2017) conclusion that *D. provincialis* is one of the most basal adapiforms. It also supports the Dunn et al. (2016) conclusions that the asiadapids found at the Vastan mines are very primitive. All four Vastan taxa appear very close together in the Matrix C trees which supports claims that the two different groups (the asiadapids and

omomyiform *Vastanomys*) were at least somewhat postcranially alike, as *Vastanomys* contains only postcranial character states in this matrix.

Conclusions

The trees alone do not necessarily support or contradict either Dunn et al. (2016) or Boyer et al. (2017)'s conclusions regarding which species best represents the crown primate ancestor. They do however show that there are significant changes to the topology of the cladograms when only postcranial data are analyzed and when new postcranial data are added to a large dataset containing multiple partitions of characters. All of the trees that contain new postcranial character states support basal placements of *D. provincialis* as well as the Vastan taxa. The fact that all of the Vastan mine species are so primitive in the results of every matrix, supports the idea that their postcranial features were similar and primitive. Further phylogenetic studies that continue to expand the datasets as well as ancestral state reconstruction analyses are the next steps to help answer questions about ancestral primate locomotion. Also, more postcranial elements of *D provincialis* are necessary to truly understand the species adaptations and behaviors. All of the craniodental characters should be scored for the additional taxa added to Matrix A to create Matrix C. Just as adding postcranial elements shifted the cladograms seen here, so to would the addition of missing craniodental character states. Having a matrix that includes all available data for *V. major* and *V. gracilis* along with the new *D. provincialis* talus would greatly enhance the current view of their placement in trees.

Despite these findings and interpretations, using only postcranial elements within a phylogenetic analysis can be problematic in that, like using only morphological data,

there are elements of the bigger picture missing. This type of phylogenetic research has the issue of being forced to rely on incomplete datasets as well as relatively subjective conclusions. Also, as technology exponentially advances, the methods used must be constantly updated. This disparity is something challenging many fields, but evolutionary anthropology is still in the midst of cohesively rectifying the large amount of knowledge with the appropriate means of organization as those means are in a constant state of improvement. The advent of software and technology should theoretically only advance our understanding, but they need to be harnessed in a meaningful and organized manner that adequately deals with previous steps taken in our understanding. Currently accepted evolutionary hypotheses and morphological interpretations of the fossil record are spread out rather than being pooled to create an analysis that includes all relevant and available information. For example, there are many studies that use phylogenetic analyses like this one, but there is not a phylogenetic analysis that includes all known character states for all known species. It should be noted that having pieces of the evolutionary mosaic is extremely beneficial and the previous contributions are immensely important. However, it should be the goal to try and efficiently organize the known fossil record and morphological insights in order to get as close to a full picture as possible. The field is already working with the disadvantage of being beholden to broken fossils and gaping unknowns - the next steps of phylogenetic research should be to fill the gaps where possible.

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Tables and Figures

Table 1.

Taxon	Associated elements
Absarokius sp.	craniodental, humerus, talus, calcaneus, and tibia
Abuqatrania basiodontos	craniodental
Adapis parisiensis	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Aegyptopithecus zeuxis	craniodental, humerus, talus, calcaneus, MT1, femur, and other postcranial elements [a]
Afradapis longicristatus	craniodental and talus
Aframonius dieides	craniodental
Afrotarsius spp.	craniodental
Algeripithecus minutus	craniodental
Allenopithecus nigroviridis	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Alouatta seniculus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Altanius orlovi	craniodental
Amphipithecus mogaungensis	craniodental
Anchomomys frontanyensis	craniodental, talus, calcaneus, and other postcranial elements [a]
Anchomomys gaillardi	craniodental
Anchomomys milleri	craniodental
Aotus trivirgatus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Apidium moustafai	craniodental
Apidium phiomense	craniodental, humerus, talus, calcaneus, tibia, femur, and other postcranial elements [a]
Arapahovius gazini	craniodental, talus, calcaneus, MT1, and other postcranial elements
Arctocebus calabarensis	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Arsinoea kallimos	craniodental
Asiadapis cambayensis	craniodental, talus, calcaneus[b], MT1[b], tibia [b], and femur [b]
Azibius trerki	craniodental and talus
Bahinia pondaungensis	craniodental
Biretia fayumensis	craniodental
Biretia megalopsis	craniodental
Branisella boliviana	craniodental
Caenopithecus lemuroides	craniodental, talus, and calcaneus
Cantius abditus	craniodental, humerus, talus, calcaneus, MT1, tibia, and femur

Cantius ralstoni	craniodental, talus, calcaneus, and other postcranial elements
Carpolestes simpsoni	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Catopithecus browni	craniodental, humerus, talus, and MT1
Cheirogaleus major	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Chipetaia lamporea	talus, calcaneus, MT1, tibia, and femur
Darwinius masillae	craniodental, humerus, calcaneus, tibia, femur, and other postcranial elements [a]
Djebelemur martinezi	craniodental and talus
Dolichocebus gaimanensis	craniodental and talus
Donrussellia provincialis	craniodental and talus
Dyseolemur pacificus	craniodental
Eosimias centennicus	craniodental and talus
Europolemur dunaifi	craniodental
Europolemur klatti	craniodental, talus, and calcaneus
Galagoides demidoff	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Galago moholi	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Hemiacodon gracilis	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Hoanghonius stehlini	craniodental and MT1
Karanisia clarki	craniodental
Komba spp.	craniodental
Lemur catta	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Lepilemur mustelinus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Leptadapis magnus	craniodental, humerus, talus, calcaneus, MT1, tibia, and other postcranial elements [a]
Leptadapis priscus	craniodental
Leptadapis ruetimeyeri	craniodental
Loris tardigradus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Loveina zephryi	craniodental
Macrotarsius montanus	craniodental
Mahgarita stevensi	craniodental
Marcgodinotius indicus	Craniodental, humerus [b], talus [b], calcaneus [b], and femur [b]
Mazateronodon endemicus	craniodental
Mescalerolemur horneri	craniodental
Microadapis sciureus	craniodental

Microcebus murinus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Microchoerus erinaceus	craniodental, humerus, calcaneus, and femur
Myanmarpithecus yarshensis	craniodental
Mytonius hopsoni	talus and calcaneus
Nannopithex abderhaldeni	craniodental, talus, calcaneus, tibia, femur, and other postcranial elements [a]
Nannopithex raabi	craniodental
Necrolemur spp.	craniodental, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Nievesia sossisensis	craniodental
Nosmips aenigmaticus	craniodental
Notharctus tenebrosus	humerus, talus, calcaneus, MT1, tibia, and femur
Nycticeboides simpsoni	craniodental and other postcranial elements [a]
Nycticebus coucang	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Oligopithecus rogeri	craniodental
Oligopithecus savagei	craniodental
Omomys sp.	craniodental, talus, calcaneus, tibia, femur, and other postcranial elements [a]
Otolemur crassicaudatus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Ourayia uintensis	talus, calcaneus, MT1, tibia, and femur
Pan troglodytes	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Parapithecus fraasi	craniodental
Parapithecus grangeri	craniodental, humerus, and talus
Perodicticus potto	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Phenacopithecus xueshii	craniodental
Plesiadapis tricuspidens	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Plesiolestes problematicus	craniodental
Plesiopithecus teras	craniodental
Pondaungia cotteri	craniodental
Pronycticebus gaudryi	craniodental
Propithecus spp.	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Propliopithecus chirobates	craniodental
Proteopithecus sylviae	craniodental
Protoadapis curvicuspidens	craniodental
Pseudoloris parvulus	craniodental
Purgatorius unio	craniodental, talus, and calcaneus
Qatrania wingi	craniodental

Rencunius zhoui	craniodental
Rooneyia viejaensis	craniodental
Saharagalago misrensis	craniodental
Saimiri sciureus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Serapia eocaena	craniodental
Shoshonius cooperi	craniodental, humerus, talus, calcaneus, MT1, tibia, and femur
Siamopithecus eocaenus	craniodental
Smilodectes gracilis	humerus, talus, and calcaneus
Steinius_spp.	craniodental and talus
Taqah propliopithecid	craniodental
Tarsius bancanus	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Tarsius sirindhornae	craniodental
Teilhardina americana	craniodental
Teilhardina asiatica	craniodental
Teilhardina belgica	craniodental, talus, calcaneus, MT1, and femur
Tetonius sp.	craniodental, talus, and calcaneus
Tupaia glis	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements [a]
Varecia variegata	craniodental, humerus, talus, calcaneus, MT1, tibia, femur, and other postcranial elements[a]
Vastanomys gracilis	humerus
Vastanomys major	humerus, talus, tibia, and femur
Wadilemur elegans	craniodental and femur
Washakius insignis	craniodental, talus, and calcaneus

Table 1: This table is a complete list of the taxa used in the phylogenetic analyses of this paper. The taxa in blue represent the species that were in the original Boyer et al. 2017 dataset and included character states for at least one of the osteological elements analyzed for the Vastan primates in Dunn et al. 2016 so they appear in all three matrixes. The taxa in orange represent the species that are not included in Matrix A and had all character states added to the matrices that they appear in: Matrix B and Matrix C. All of the uncolored taxa only appear in Matrix A.

a Other postcranial element refers to other osteological elements that were included in the original dataset but are not discussed in the Dunn et al. 2016 paper so they were excluded from Matrix B.

b These elements had associated character states in Matrix A that were edited or added due to new specimens outlined in the Dunn et al. 2016 research. These changes are not contained within Matrix A and do not affect the results of running this matrix in TNT or the resulting tree.

Table 2.

Taxon	Associated elements	Functional References used for Character scores
Absarokius sp.	humerus, talus, calcaneus, and tibia	
Adapis parisiensis	humerus, talus, calcaneus, MT1, tibia, and femur	
Aegyptopithecus zeuxis	humerus, talus, calcaneus, MT1, and femur	
Afradapis longicristatus	talus	
Allenopithecus nigroviridis	humerus, talus, calcaneus, MT1, tibia, and femur	
Alouatta seniculus	humerus, talus, calcaneus, MT1, tibia, and femur	
Anchomomys frontanyensis	talus and calcaneus	
Aotus trivirgatus	humerus, talus, calcaneus, MT1, tibia, and femur	
Apidium phiomense	humerus, talus, calcaneus, tibia, and femur	
Arapahovius gazini	talus, calcaneus, and MT1	
Arctocebus calabarensis	humerus, talus, calcaneus, MT1, tibia, and femur	
Asiadapis cambayensis [b]	talus, calcaneus, MT1, tibia, and femur	Dunn et al. 2016; Rose et al. 2009
Azibius trerki	talus	
Caenopithecus lemuroides	talus and calcaneus	
Cantius abditus	humerus, talus, calcaneus, MT1, tibia, and femur	
Cantius ralstoni	talus and calcaneus	
Carpolestes simpsoni	humerus, talus, calcaneus, MT1, tibia, and femur	
Catopithecus browni	humerus, talus, and MT1	
Cheirogaleus major	humerus, talus, calcaneus, MT1, tibia, and femur	
Chipetaia lamporea [a]	talus, calcaneus, MT1, tibia, and femur	
Darwinius masillae	humerus, calcaneus, tibia, and femur	
Djebelemur martinezi	talus	
Dolichocebus gaimanensis	talus	
Donrussellia provincialis	talus	Boyer et al. 2017
Eosimias centennicus	talus	
Europolemur klatti	talus and calcaneus	
Galagoides demidoff	humerus, talus, calcaneus, MT1, tibia, and femur	
Galago moholi	humerus, talus, calcaneus, MT1, tibia, and femur	
Hemiacodon gracilis	humerus, talus, calcaneus, MT1, tibia, and femur	
Hoanghonius stehlini	MT1	
Lemur catta	humerus, talus, calcaneus, MT1, tibia, and femur	
Lepilemur mustelinus	humerus, talus, calcaneus, MT1, tibia, and femur	
Leptadapis magnus	humerus, talus, calcaneus, MT1, and tibia	
Loris tardigradus	humerus, talus, calcaneus, MT1, tibia, and femur	

Marcgodinotius indicus [b]	humerus, talus, calcaneus, and femur	Dunn et al. 2016; Rose et al. 2009
Microcebus murinus	humerus, talus, calcaneus, MT1, tibia, and femur	
Microchoerus erinaceus	humerus, calcaneus, and femur	
Mytonius hopsoni [a]	talus and calcaneus	Dunn 2009; Dunn 2010
Nannopithex abderhaldeni	talus, calcaneus, tibia, and femur	
Necrolemur spp.	talus, calcaneus, MT1, tibia, and femur	
Notharctus tenebrosus [a]	humerus, talus, calcaneus, MT1, tibia, and femur	Boyer and Seiffert 2013; Chester 2015; Dunn 2009; Gebo 1988; Gregory 1920; Morphosource image for Specimen AMNH 131945 and AMNH 11474
Nycticebus coucang	humerus, talus, calcaneus, MT1, tibia, and femur	
Omomys sp.	talus, calcaneus, tibia, and femur	
Otolemur crassicaudatus	humerus, talus, calcaneus, MT1, tibia, and femur	
Ourayia uintensis [a]	talus, calcaneus, MT1, tibia, and femur	Boyer and Seiffert 2013; Dunn et al. 2006; Dunn 2009; Dunn 2010;
Pan troglodytes	humerus, talus, calcaneus, MT1, tibia, and femur	
Parapithecus grangeri	humerus and talus	
Perodicticus potto	humerus, talus, calcaneus, MT1, tibia, and femur	
Plesiadapis tricuspidens	humerus, talus, calcaneus, MT1, tibia, and femur	
Propithecus spp.	humerus, talus, calcaneus, MT1, tibia, and femur	
Purgatorius unio	talus and calcaneus	
Saimiri sciureus	humerus, talus, calcaneus, MT1, tibia, and femur	
Shoshonius cooperi	humerus, talus, calcaneus, MT1, tibia, and femur	
Smilodectes gracilis [a]	humerus, talus, and calcaneus	Boyer and Seiffert 2013; Gebo 1988; Dunn 2009; Morphosource image for Specimen AMNH 131774
Steinius_spp.	talus	
Tarsius bancanus	humerus, talus, calcaneus, MT1, tibia, and femur	
Teilhardina belgica	talus, calcaneus, MT1, and femur	
Tetonius sp.	talus and calcaneus	
Tupaia glis (designated outgroup)	humerus, talus, calcaneus, MT1, tibia, and femur	
Varecia variegata	humerus, talus, calcaneus, MT1, tibia, and femur	
Vastanomys gracilis [a]	humerus	Dunn et al. 2016
Vastanomys major [a]	humerus, talus, tibia, and femur	Dunn et al. 2016, Morphosource scan for Specimen GU 800

Wadilemur elegans	femur	
Washakius insignis	talus and calcaneus	

Table 2:
This table is a closer examination of what is included in Matrix B specifically and shows which osteological elements had character states within this dataset. Also shown, are references that pertain to certain species and were relevant to the creation of this matrix.
[a] These taxa were not in the Matrix A taxon list and were completely added to the dataset.
[b] These taxa were already within Matrix A, but additional character states were added.

Table 3.

Tree	Matrix	Software	Description	# of Characters	# of Taxa	Best Score	# of MPT	Tree support method
A	Boyer et al. 2017	TNT	Includes only taxa, characters, and character states in the dataset that was created by Boyer et al. 2017.	389	110	4664	16	n/a
B	Postcranial only	TNT	Includes taxa from Boyer et al. 2017 matrix with character states for postcranial elements described in Dunn et al. 2016 along with additional seven taxa*.	101	64	929	11	Bootstrap
C	Boyer et al. 2017 + Postcranial	TNT	Includes all taxa and characters from the Boyer et al. 2017 dataset along with the seven addition taxa* and character states from the postcranial matrix added in.	389	117	4724	23	Bootstrap

Table 3:
This table outlines the cladistic results for this project. Each of the three matrices were run with the same TNT settings and with the same molecular scaffold constraint.
Abbreviation: **MPT**= most parsimonious trees
*The additional taxa are *V. major, V. gracilis, N. tenebrosus, S. gracilis, O. uintensis, C. lamporea,* and *M. hopsoni.* These seven additional species are outlined in the Introduction and Methods section.

Matrix A:

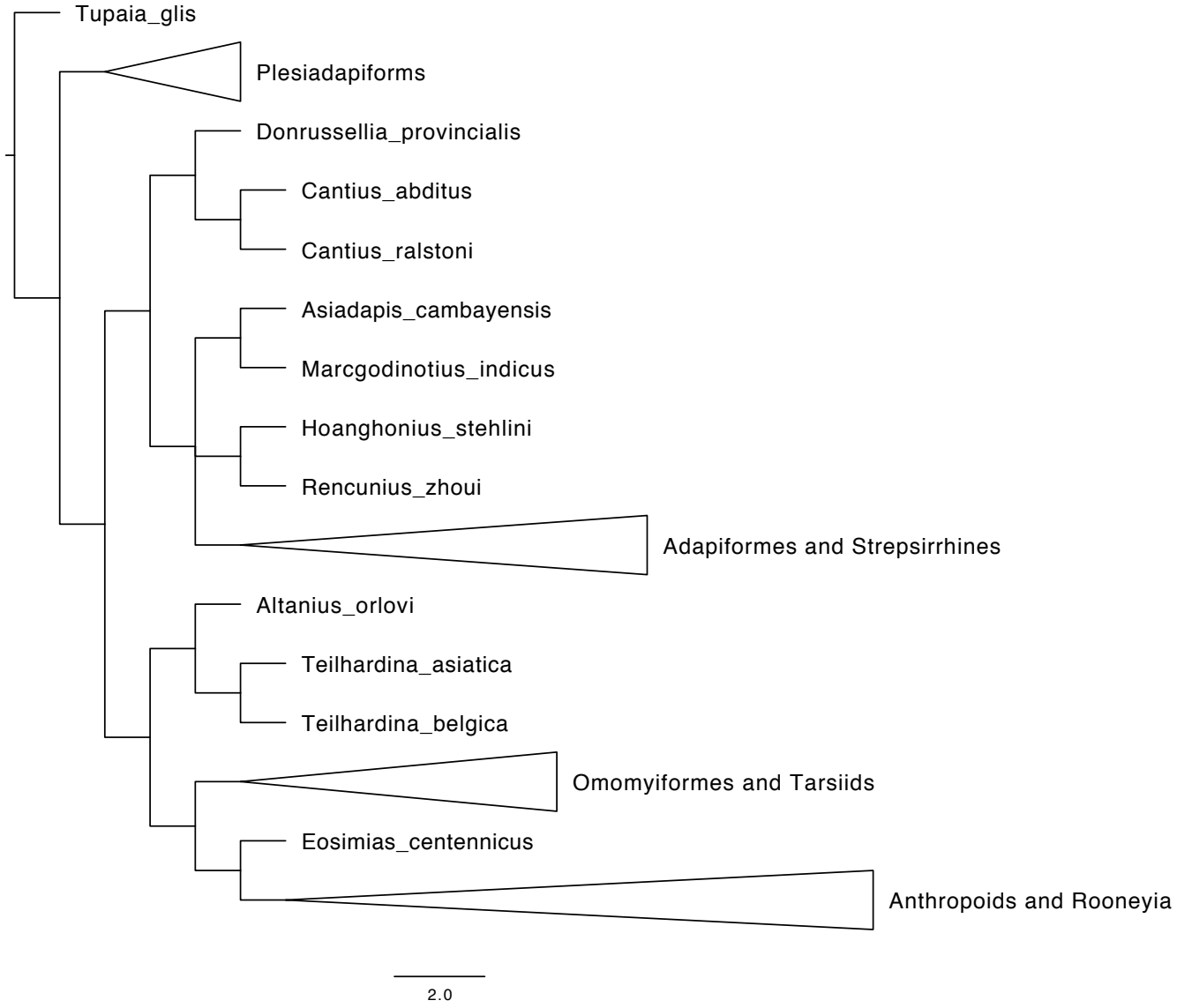

Figure 1a.
This is the resulting strict consensus tree from the tree search of Matrix A in TNT that has some taxa grouped together for simplification.

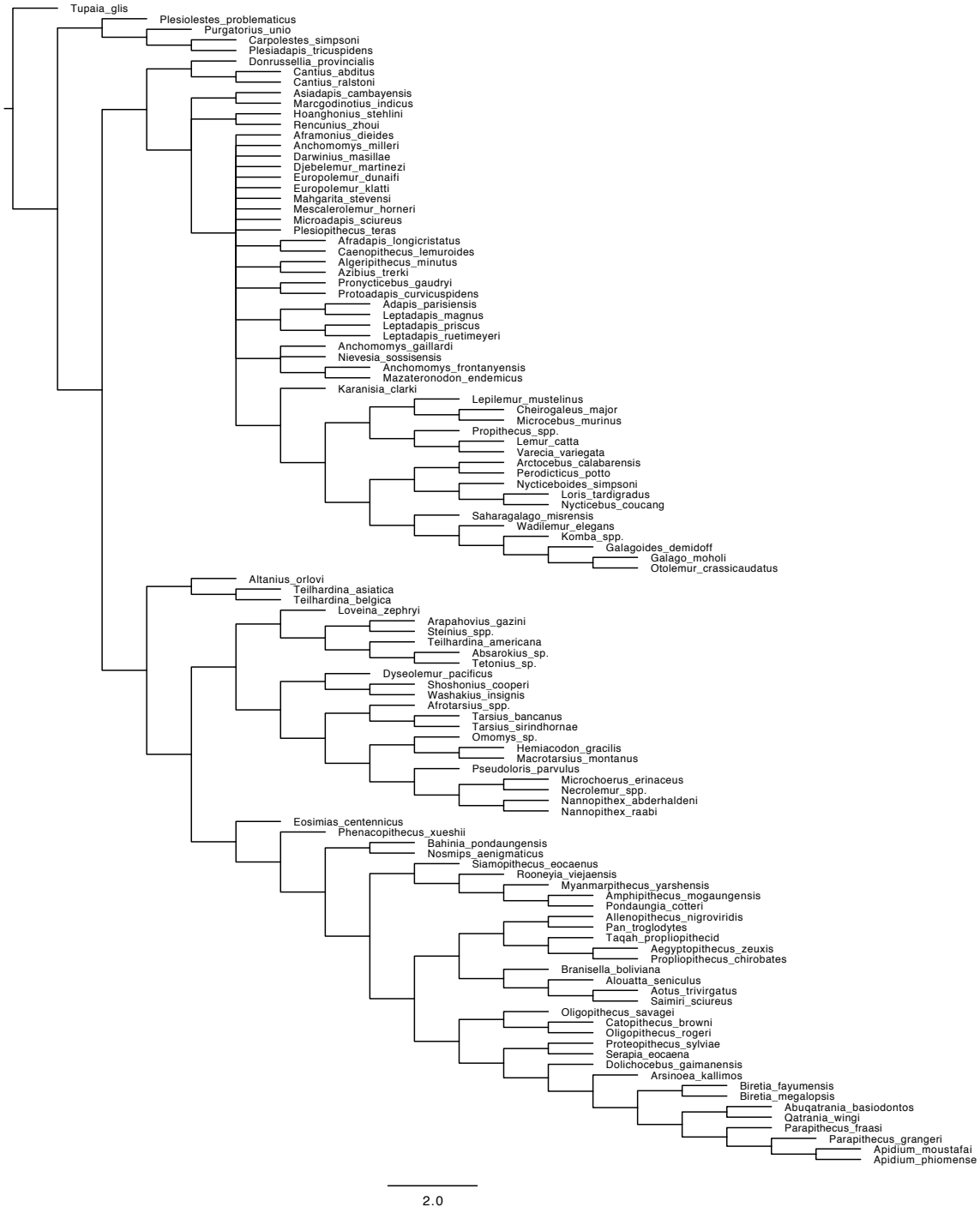

Figure 1b.
This is the same strict consensus tree as Figure 1a. but completely expanded to show all taxa.

Matrix B

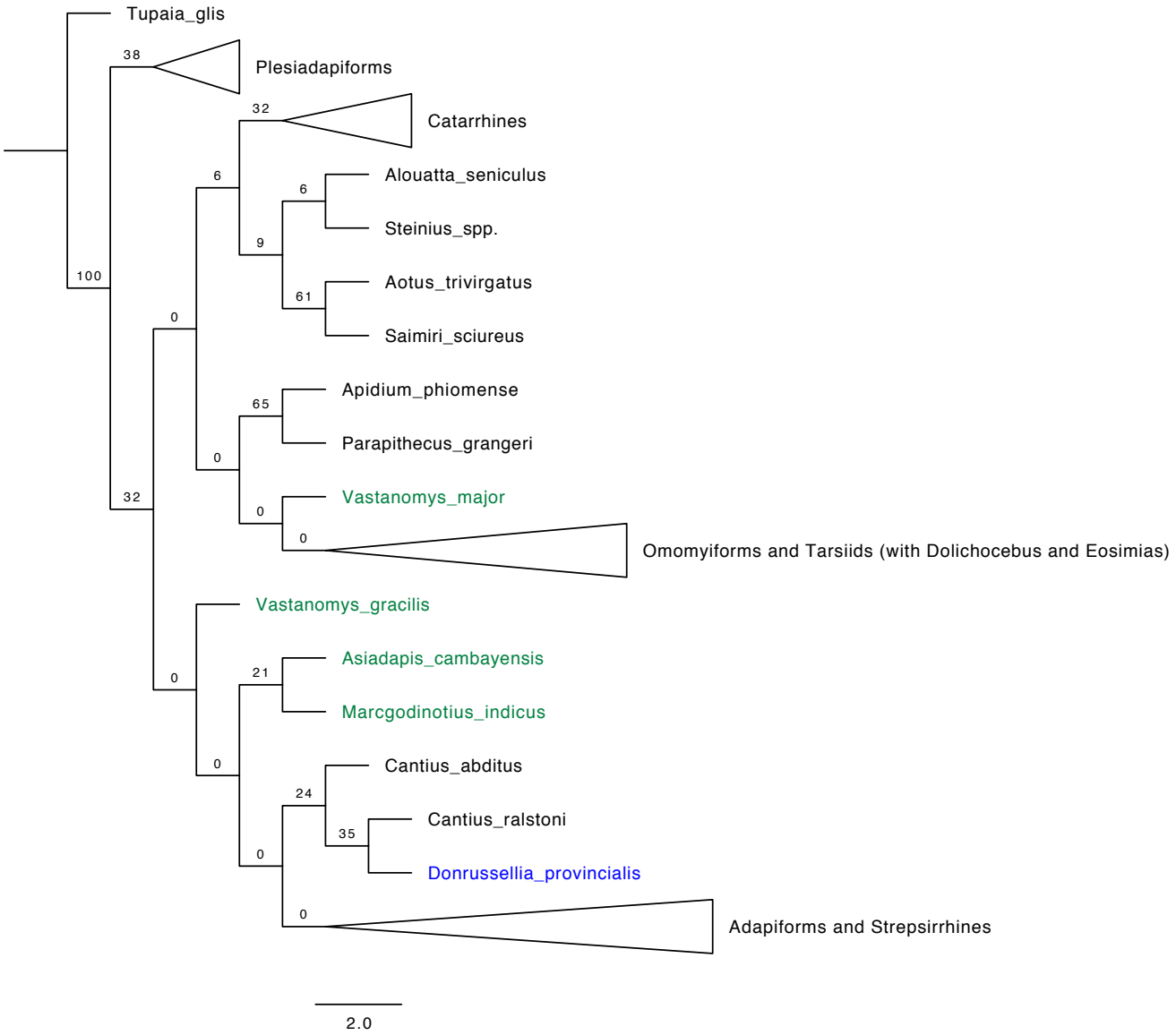

Figure 2a.
This is the resulting strict consensus tree from the tree search of Matrix B in TNT that has some taxa grouped together for simplification.
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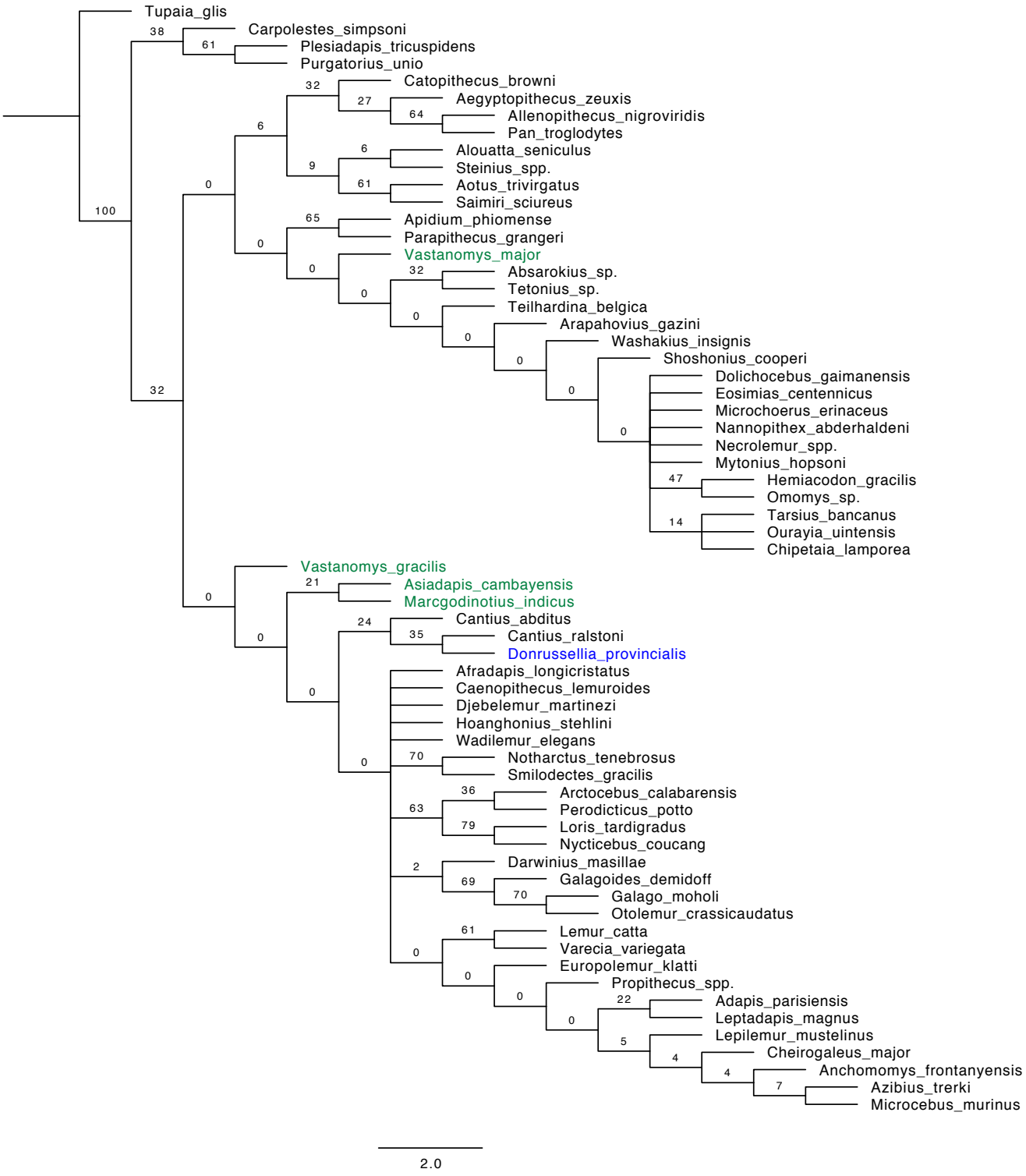

Figure 2b.
This is the same strict consensus tree as Figure 2a. but completely expanded to show all taxa.

Matrix C:

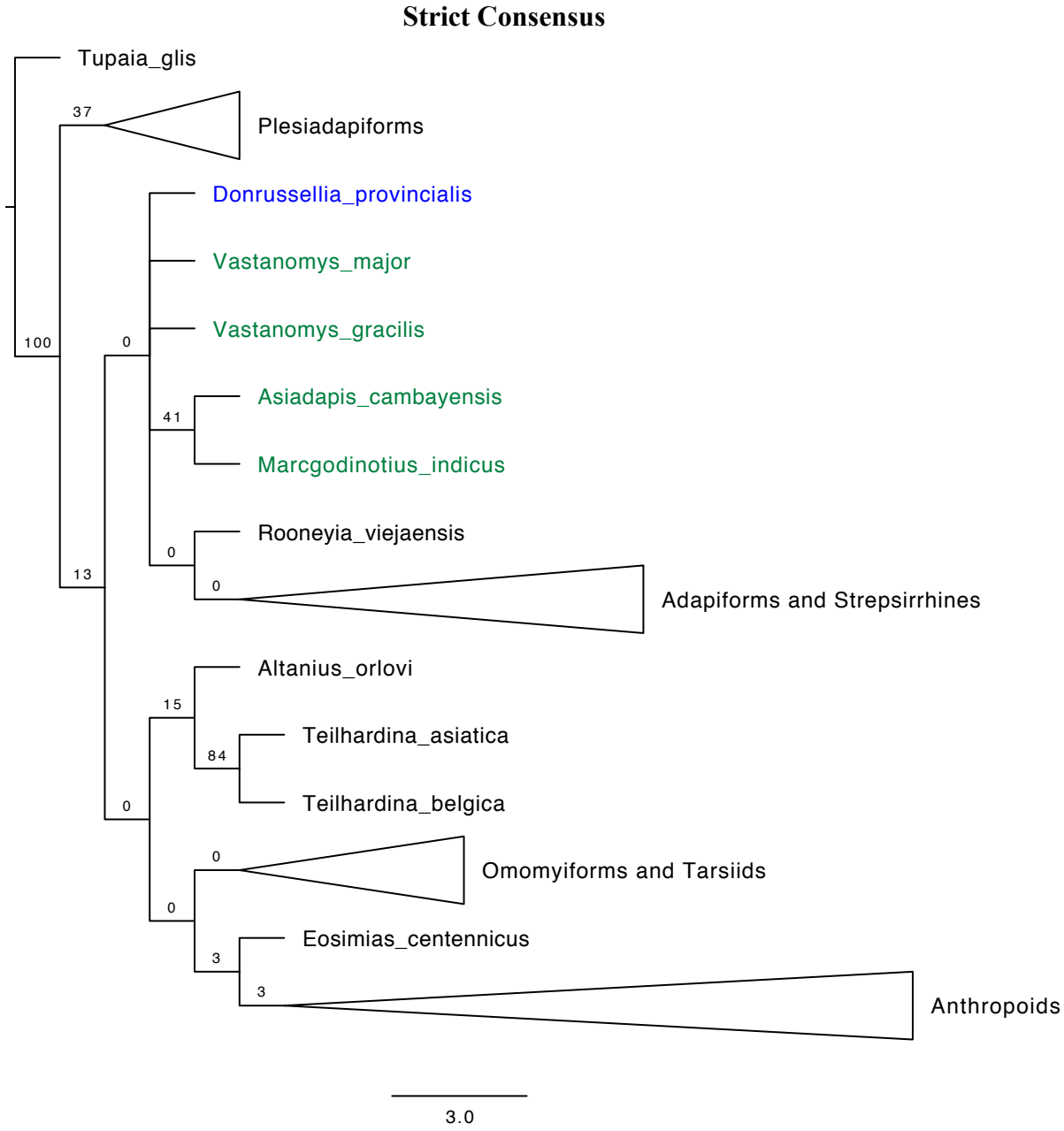

Figure 3a.
This is the resulting strict consensus tree from the tree search of Matrix C in TNT that has some taxa grouped together for simplification.

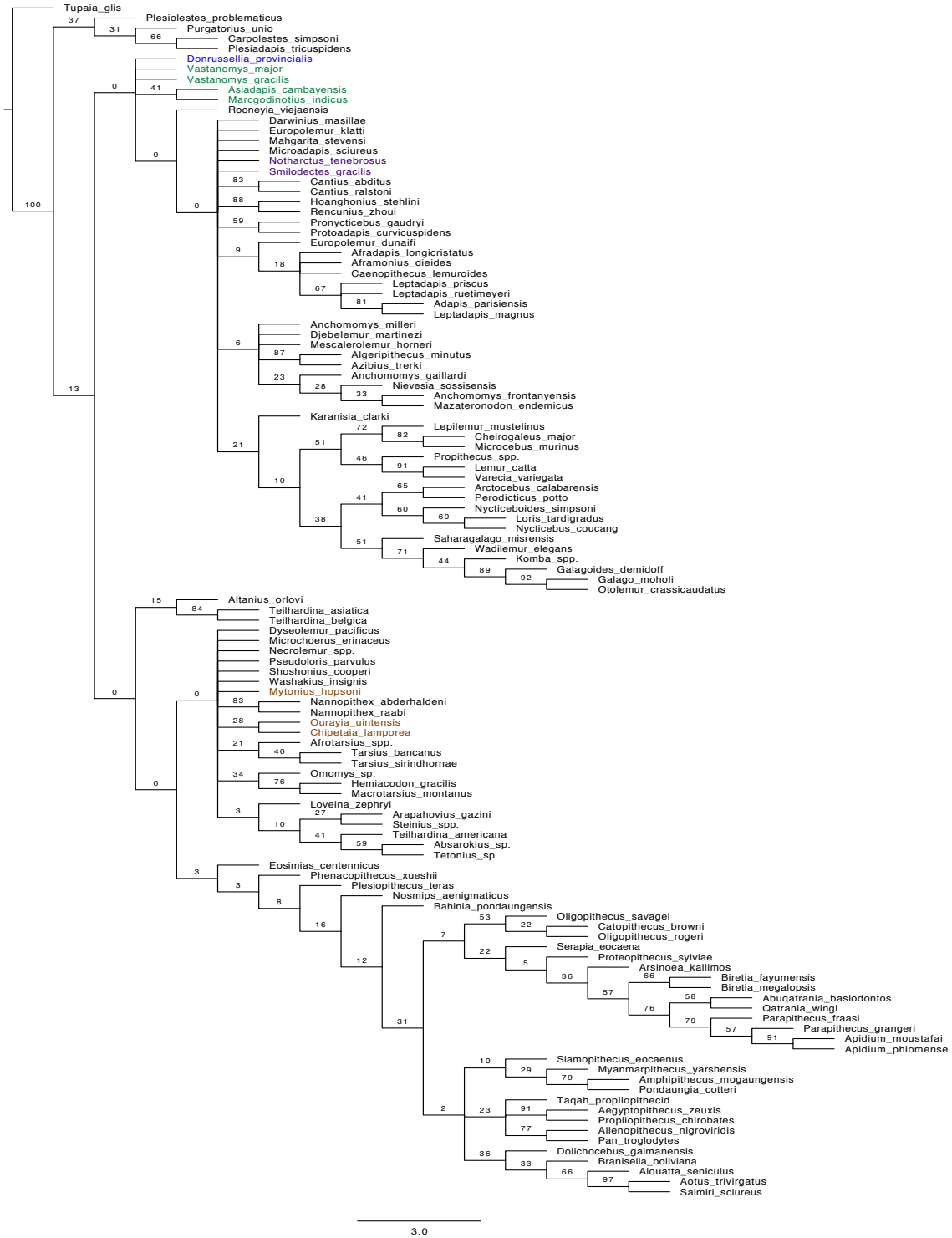

Figure 3b.
This is the same strict consensus tree as Figure 3a. but completely expanded to show all taxa.

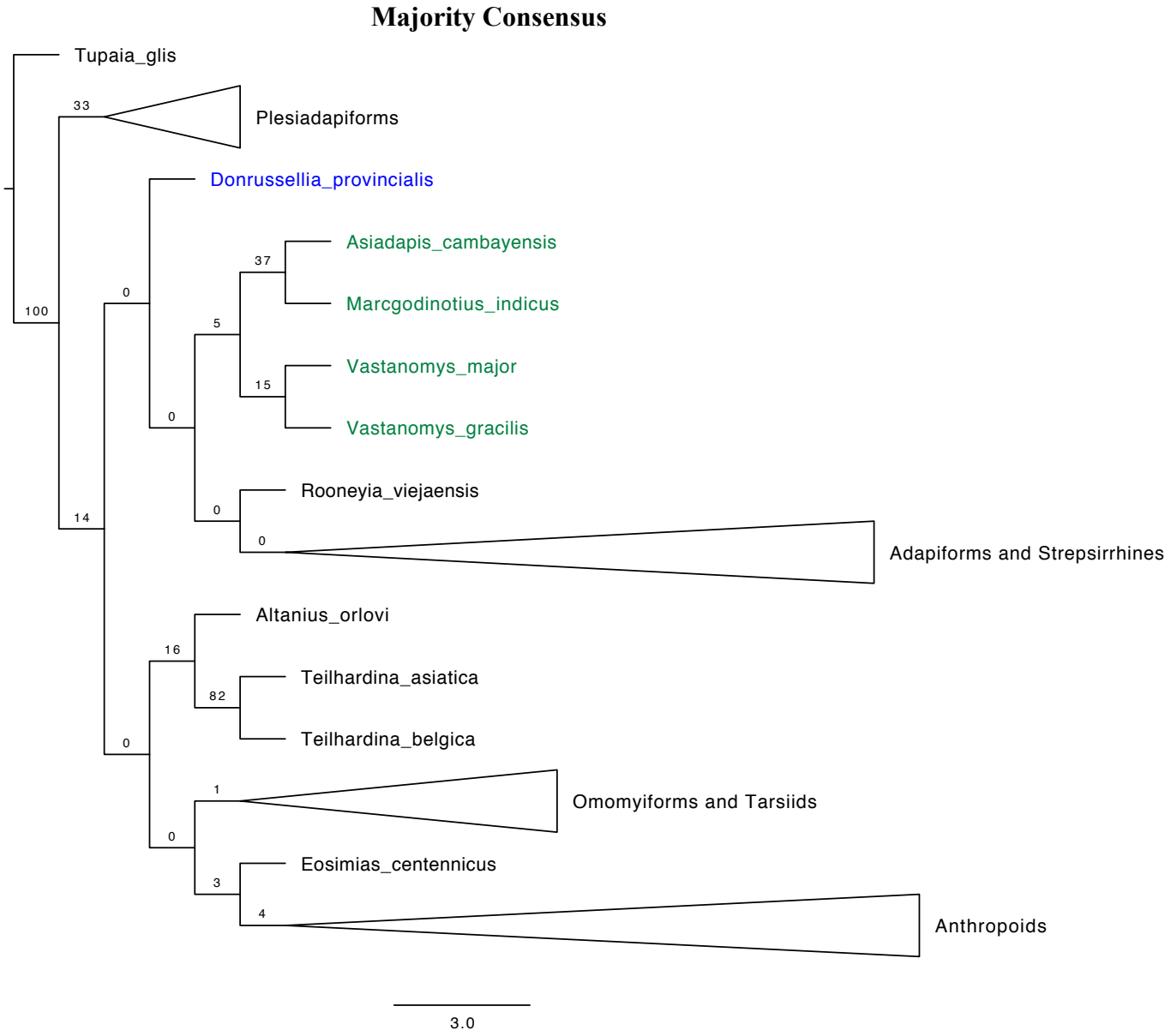

Figure 4a.
This is the resulting majority consensus tree from the tree search of Matrix C in TNT that has some taxa grouped together for simplification.]

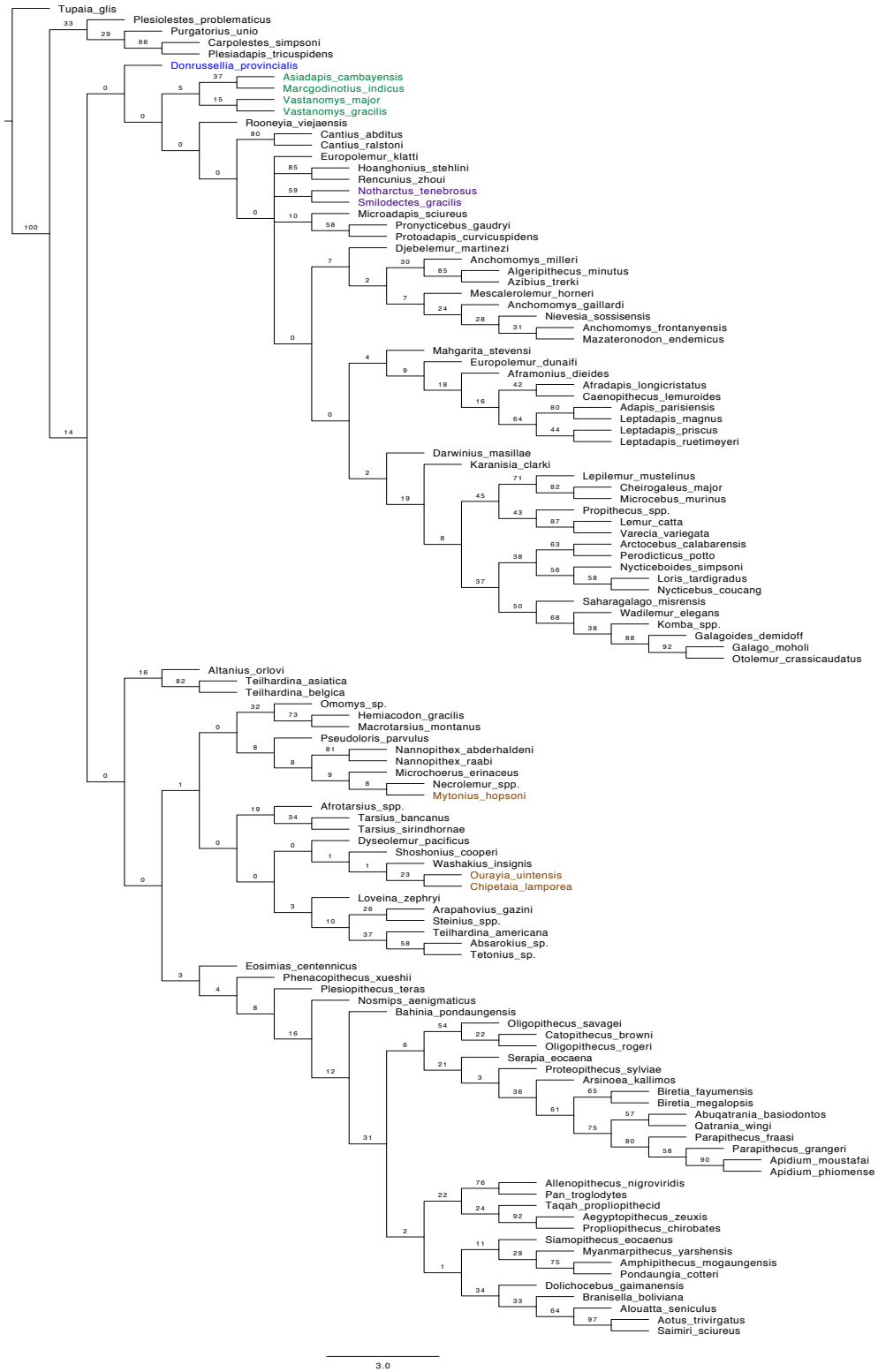

Figure 4b.
This is the same majority consensus tree as Figure 4a. but completely expanded to show all taxa.